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The distribution of invasive *Pennisetum setaceum* along roadsides in western South Africa: the role of corridor interchanges

S J RAHLAO*, S J MILTON*†, K J ESLER* & P BARNARD†‡

*Department of Conservation Ecology and Entomology, Centre for Invasion Biology, Stellenbosch University, Matieland, South Africa, †DST Centre of Excellence, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa, and ‡Climate Change and BioAdaptation Division, Kirstenbosch Research Centre, South African National Biodiversity Institute, Claremont, South Africa

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Summary

Roads and rivers may be dispersal corridors for invasive alien grass seeds that fly and float. These two systems interact at bridge interchanges that are also disturbed artificial habitats. The invasive grass *Pennisetum setaceum* (perennial fountain grass) establishes on roadsides and river banks and benefits from habitat conditions prevailing at these interchanges. The distribution of the grass across biomes and vegetation types and the influence of environmental variables were assessed. A road survey method was used to record and map the distribution of *P. setaceum* along 1 km roadside transects at 10 km intervals and at every road-river corridor interchange for 5112 km of South African national roads in the arid and semi-arid parts of the country. *Pennisetum setaceum* populations occurred in 10% of the total length sampled, including the interchanges. Fynbos Swartland Shale Renosterveld was the most significantly invaded amongst the vegetation types surveyed. Our results indicate that, although *P. setaceum* performs better on the interchanges, it does not preferentially colonise them over other parts of the landscape. The presence of *P. setaceum* was, however, closely associated with the presence of water bodies and disturbances away from the roads. Corridor interchanges should be considered important targets of both local and regional efforts to prevent and control *P. setaceum* invasions.

Keywords: disturbance, invasive alien species, inflorescence, management, ornamental grass, perennial grasses, road survey.

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Introduction

Roadsides in some cases act as corridors for spread of invasive alien species into natural ecosystems (Gelbard & Belnap, 2003; Christen & Matlack, 2006; Jodoin *et al.*, 2008). The disturbed conditions at roadsides promote the establishment of invasive species (Harrison *et al.*, 2002; Dong *et al.*, 2008). Water shed from roads (O'Farrell & Milton 2006) increases the availability of water and nutrients on road verges, which can increase plant success (Rahlao *et al.*, 2010) along these corridors (Lamont *et al.*, 1994). The improvement of roads leads to the widening of cleared areas adjacent to roads (verges) and an increase in the number of invasive alien species that exploit disturbance opportunities (Gelbard & Belnap, 2003; Kalwij *et al.*, 2008).

Rivers are also considered habitats and corridors for invasive alien species into ecosystems (Pyšek & Prach, 1993; Johansson *et al.*, 1996; Stohlgren *et al.*, 1998) and may also act as sources of invasive alien species

Correspondence: Sebataolo J Rahlao, Energy Research Centre, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa. Tel: (+27) 21 650 2831; Fax: (+27) 21 650 2830; E-mail: sebataolo.rahlao@uct.ac.za, srahlao@sun.ac.za

(Pulliam, 1988; Bang *et al.*, 2007). The continuous availability of water and nutrients as well as periodic flooding create disturbances that make riparian zones suitable for establishment of invasive alien plant species (Planty-Tabacchi *et al.*, 1996; Stohlgren *et al.*, 1998; Hood & Naiman, 2000).

Pennisetum setaceum (Forssk.) Chiov is an invasive C4 perennial bunchgrass native to the North African arid Mediterranean area of the Atlas Mountains and the Middle East (Williams *et al.*, 1995). Introduced in many parts of the world as an ornamental plant and for soil stabilisation, it has escaped from horticulture into many natural and semi-natural habitat types (Williams *et al.*, 1995; Milton *et al.*, 1998; Henderson, 2001; Joubert & Cunningham, 2002), across broad altitudinal ranges (Tunison, 1992; Williams *et al.*, 1995) and varying rainfall and water conditions (Williams & Black, 1994; Joubert & Cunningham, 2002), as well as varying soil types (Milton *et al.*, 1998). *P. setaceum* was introduced to South Africa around the 1930s (L Henderson, pers. comm.). It is apomictic and is capable of wide phenotypic variation (Williams *et al.*, 1995). Although it reproduces mainly by seed, it forms pseudo-vivipary plantlets when inflorescences are inundated (Milton *et al.*, 2008). The light seeds are dispersed in feathery spikelets, drifting in the wind or floating on water. Its popularity in horticulture and successful spread is probably due to its drought tolerance, unpalatability to animals, rapid growth and profuse seed production (Milton *et al.*, 1998; Cabin *et al.*, 2000). It has been declared a Category 1 invasive weed under the South African Conservation of Agricultural Resources Act, 1983 (CARA amended in 2001) and as such must be controlled.

Disturbance prone rivers and roads provide a source of invasive alien species propagules that may eventually escape into the neighbouring landscapes (Parendes & Jones, 2000; Pyšek *et al.*, 2007; Richardson *et al.*, 2007). The multiple functions of roads and rivers in facilitating invasion have been documented independently for each corridor type. No previous studies have examined the effect of interaction of roads and rivers on invasion success. This study addresses the effect of the interaction of these corridors at the interchanges (road bridges across rivers) in facilitating invasion. To determine the environmental factors that best explain the distribution of *P. setaceum* in semi-arid regions, we tested the hypotheses that (i) *P. setaceum* invasion differs among South African biomes and vegetation types, (ii) the grass performs better and is more abundant at road-river interchanges than other parts of the landscape, and (iii) is associated with disturbances, such as settlements and cultivation, but not rangelands along the roads.

Methods

A single observer used the drive-by survey method (Milton & Dean, 1998) that made use of overland long-distance journeys to record the presence and absence of the grass at 10 km fixed intervals for 5112 km along the pre-selected major roads in the arid and semi-arid regions of South Africa. The survey route traversed Albany Thicket (n = 21 sites), Azonal vegetation (n = 56), Fynbos (n = 147), Grassland (n = 86), Nama Karoo (n = 187), Arid Savanna (n = 78), and Succulent Karoo (n = 51) (Fig. 1). The survey routes were selected based on previously recorded occurrences of *P. setaceum* within South Africa (Henderson, 1995; Milton & Dean, 1998; Milton *et al.*, 1998; Bromilow, 2001).

Roadsides are surveyed because they are susceptible to invasion and are accessible for sampling (Milton & Dean, 1998). Roadside surveys have been particularly useful and cost effective for large scale and rapid assessment of invasive species distribution across southern Africa (Milton & Dean, 1998; Milton *et al.*, 1998; Joubert & Cunningham, 2002) and elsewhere (Parendes & Jones, 2000; Trombulak & Frissell, 2000; Gelbard & Belnap, 2003). Surveys took place from October 2006 to October 2007. Each transect and interchange was classified according to biome, vegetation type/units, rainfall seasonality and annual rainfall. These data were obtained from Mucina and Rutherford (2006).

The survey was divided into two parts: (i) every 10 km, the presence or absence of *P. setaceum* in a 1 km transect was recorded, and (ii) if there was a road-river interchange before the end of 10 km, that interchange was surveyed, starting the next 10 km strip thereafter. This means that the surveyed strips were sometimes less than 10 km apart, if a road-river interchange was intercepted within the strip. The road-river interchanges were considered to mark the beginning of the next 10 km strip. The GPS coordinates of all transects, including the road-river interchanges, were captured in a GPS Garmin Version 2.01. In every sample where the grass was present, additional information on the grass population density (number of individuals per square meter) and performance (basal diameter, height and number of inflorescences) was collected in a belt transect (10×2 m) along the road verge or road-river exchange. The basal diameter, length of the longest living leaf and the number of inflorescences were recorded from a sample of 10 individual plants to determine growth and reproductive performance. The landscape features were also recorded: land-use adjacent to the roadside, soil surface type, vegetation type and biome, mean annual rainfall and rainfall seasonality. The GPS coordinates

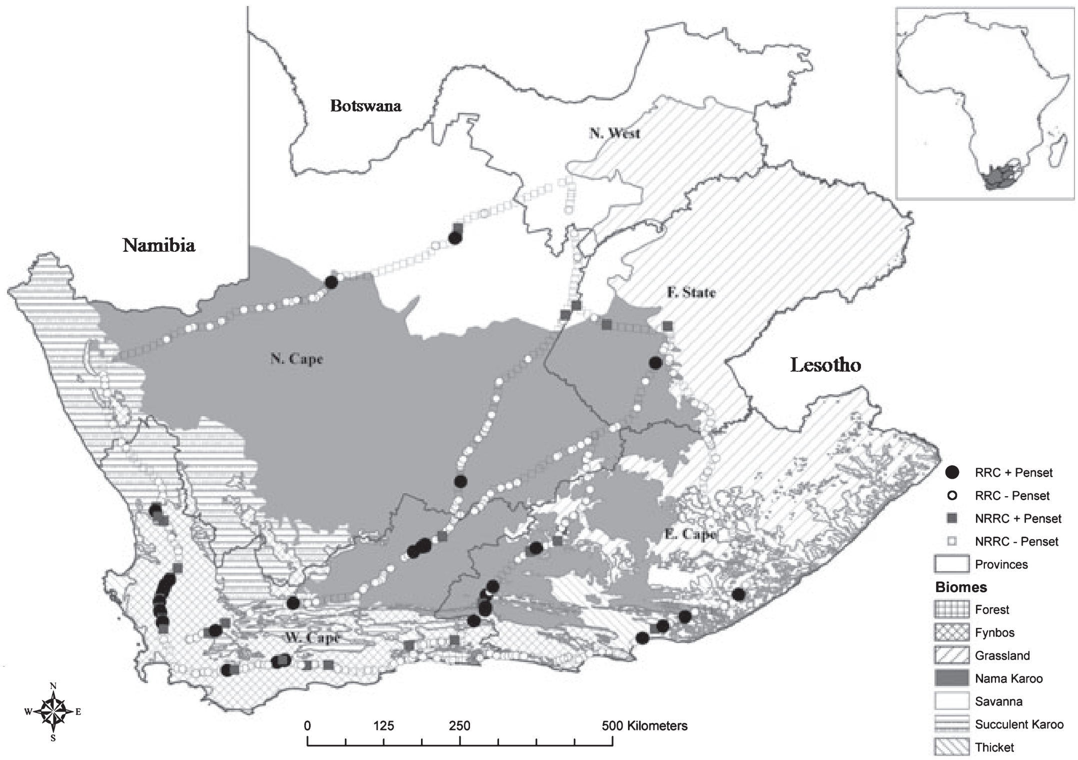

Fig. 1 Routes travelled during the road survey and records of *Pennisetum setaceum* (fountain grass) in the western parts of South Africa. RRC (+) and RRC (–) indicate road-river interchanges (RRC) with and without *P. setaceum* respectively. NRRC (–) and NRRC (+) indicate non-road-river interchanges (NRRC) with and without *P. setaceum* respectively.

and the landscape features of sample sites were recorded, regardless of the presence or absence of *P. setaceum*.

Analysis of variance (ANOVA) was performed in STATISTICA version 8 (Statsoft, 2007) to assess differences between plant basal diameters, plant height, number of inflorescences and density (number of individuals per square metre). Land use types, soil types and rainfall season were coded numerically for regression analysis to compare the frequency of *P. setaceum* occurrence. Chi-square tests were used to test for differences in the proportion of interchanges along the surveyed roads with and without *P. setaceum* and to test its association with certain vegetation types. Generalised linear models were used to assess the effect of road-river interchange, rainfall amount and biome type, land use and vegetation type on plant performance (basal diameter). Factors and interactions that did not affect the occurrence and performance of *P. setaceum* were excluded from further analyses. The non-parametric Mann–Whitney *U*-test was used to compare the performance of *P. setaceum* on the interchanges and non interchanges along the surveyed major roads when the data were not normally distributed. Differences in occurrences of *P. setaceum* per transect were compared among soil types, biomes and rain seasons using ANOVA and the *post hoc* Bonferroni test. To test whether the occurrence of *P. setaceum* was strongly influenced by rain season, soil type and land use, the frequencies of occurrence were compared with distribution of transects for each of the variables.

Results

Comparative reproductive performance of P. setaceum *across the landscape*

Pennisetum setaceum showed no significant habitat preference for either road-river interchanges or other parts of the landscape across biomes ($\chi^2 = 0.652$, d.f. = 1, $P = 0.419$). However, when the grass occurred on interchanges, it performed better ($F_{(1,64)} = 15.618$, $P < 0.001$), with larger basal diameters than in the other parts of the landscape. In addition, the number of inflorescences per individual plant was higher (Mann–Whitney *U*-test, $Z = 3.237$, $P < 0.01$) on the interchanges than in other parts of the landscape. However, the density (number of individuals per square meter) was not different between the road-river interchanges and the rest of the landscape (Mann–Whitney *U*-test, $Z = 0.698$, $P = 0.485$). The amount of rainfall and the biome type did not influence plant performance across the landscape in the sampled areas and during the study period (Table 1).

Table 1 Univariate test of different variable significance for plant performance (Basal diameter) using generalised linear models. RRC, road-river interchange

Effect	DF	SS	MS	F	P	Significance
Rain (mm)	1	108.51	108.51	2.105	0.153	NS
Biome	6	252.58	42.09	0.817	0.563	NS
RRC	1	503.12	503.12	9.763	0.003	***
Biome × RRC	6	228.24	38.04	0.738	0.621	NS
Error	51	2628.09	51.53			

Pennisetum setaceum *distribution and frequency between biomes types*

A total of 322 transects and 301 interchanges were recorded along 5112 km of major roads in semi arid South Africa (Fig. 1). *P. setaceum* populations occurred in about 10.5% (n = 66) of the total (n = 629) transects and interchanges. The number of transects surveyed differed between biomes. The percentages of transects invaded per biome were 24% (n = 21) for Albany Thicket, 13% (n = 56) for Azonal vegetation, 18% (n = 147) for Fynbos (including Renosterveld), 3% (n = 86) for Grassland, 7% (n = 187) for Nama Karoo, 6% (n = 78) for Savanna and 14% (n = 51) for Succulent Karoo (Fig. 2). Within biomes, *P. setaceum* occurred at different frequencies among vegetation types; e.g. the Swartland Shale Renosterveld vegetation type was invaded more frequently (80%) (M-L χ^2 = 82.322, d.f. = 100, P < 0.001) than other Fynbos vegetation types. Although highly sampled (56 transects), the Nama Karoo vegetation type, known as 'Gamka Karoo', was less invaded (2%).

Environmental factors affecting P. setaceum *occurrence*

Our results show that *P. setaceum* occurrence was not influenced ($F_{(2,626)}$ = 2.3898, P = 0.092) by any of the three land use types recorded (Table 2). In addition, the land use type did not affect *P. setaceum* performance (basal diameter) ($F_{(2,63)}$ = 0.14012, P = 0.870) across the landscape during the survey period. Most of the sample transects (95%) were associated with fine textured soil and 4% with alluvium soils (Table 2), but the presence of *P. setaceum* was not statistically associated with any soil type (M-L χ^2 = 2.417, P = 0.490). However, plants performed better (larger in size) on alluvium soils than on fine textured soils ($F_{(1,63)}$ = 7.1584, P < 0.01). The amount of rainfall in these arid areas did not influence the size of plants (basal diameter) (R = −0.0425, P = 0.287) throughout the surveyed routes. Although most (56%) sample transects occurred in the summer rainfall regions, the winter rainfall region was more invaded (39%) than the other rain season regions (Table 2). Plant sizes (basal diameter) were, however, not different among the rain seasons ($F_{(2,63)}$ = 0.32699, P = 0.72).

Discussion

Distribution of P. setaceum *between biomes and vegetation types*

Pennisetum setaceum was present in 10% (66/629) of the surveyed distance/points with other similar habitats not yet invaded, suggesting that it is an emerging invader in South Africa. This is despite it being classified as a category 1 weed and invader (Henderson, 2001). Our results show the Fynbos biome to be relatively more invaded (41%) by *P. setaceum* and this is in agreement with results of Milton and Dean (1998). The abundance of *P. setaceum* in the Swartland Shale Renosterveld habitat of the Fynbos biome could be attributed to this area having a winter rainfall, Mediterranean-type climate that closely matches the conditions from which this grass originates (Milton *et al*., 1998). In addition, this area has relatively nutrient rich soils and it is highly

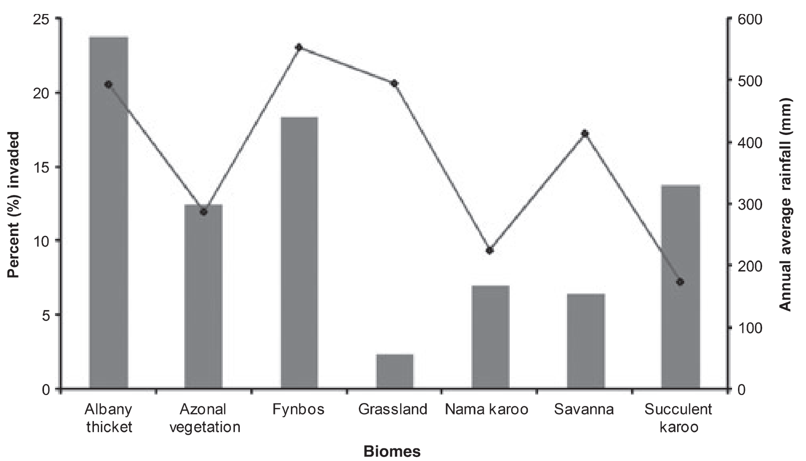

Fig. 2 The percentage (bars) of invaded transects across biomes along the sampled roadsides and the average annual average rainfall (lines) at each biome. The forest and desert biomes were excluded from these analyses due to few (< 2) sampled transects.

Table 2 Relative frequencies (%) of *Pennisetum setaceum* occurrence with respect to the different variables along the sample transects and road-river interchanges in arid and semi-arid parts of South Africa

Variable	Transect samples	Occurrence: River interchange	Occurrence: Non-river interchange	Invaded: River interchange	Invaded: Non-river interchange	Total invaded (%)
Rain season						
Mixed	25	32	19	31	29	30
Summer	56	50	62	31	29	30
Winter	19	18	19	37	42	39
Soil						
Alluvium	4	8	1	6	0	3
Fine	95	92	98	91	100	96
Rock	0	0	0	0	0	0
Sand	1	0	0	3	0	1
Biome						
Albany Thicket	3	4	3	9	6	7
Azonal Vegetation	9	15	3	14	6	11
Fynbos	23	23	24	31	52	41
Grassland	14	13	15	3	3	3
Nama Karoo	30	32	28	26	13	20
Savanna	12	5	19	3	13	7
Succulent Karoo	8	8	8	14	6	11
Land use						
Cultivated	12	11	12	29	39	33
Ranched	59	56	63	37	32	35
Settled	29	33	25	34	29	32

transformed into cropland and vineyards, due to prime quality of the land for these agricultural purposes (Mucina & Rutherford, 2006). This result is also in agreement with other studies that found *P. setaceum* to be confined largely to shale and granite formations along the Cape Peninsula (Milton *et al.*, 1998).

Factors affecting P. setaceum *performance on the interchanges*

Although the occurrence of *P. setaceum* was not determined by the presence of road river interchanges, the grass growth (basal diameter) and reproductive (inflorescence number) performance was higher for plants on these interchanges than in other parts of the landscape. A number of factors could support this improved performance on the interchanges. Firstly, the maintenance of the road network (mowing and ditch digging) could facilitate resource availability and hence rapid growth of the grass. These activities create disturbances for establishment of openings for colonisation and, if soil conditions and climate are suitable, *P. setaceum* will establish if propagules arrive there. Secondly, the soil used as land fill for bridge construction over rivers could be suitable for the establishment of *P. setaceum* propagules. Thirdly, the introduction of soil from elsewhere into the new location during road and bridge construction, introduce unsuitable conditions for indigenous species and hence *P. setaceum* may establish without any competition. Fourthly, there could be a continuous supply of moisture, due to drainage ditches along roads (Jodoin *et al.*, 2008) and possibly nutrients as a result of debris deposited on the side bridge, particularly during flooding and this might support the establishment and success of *P. setaceum* on these interchanges. Lastly, the road-river interchanges are relatively inaccessible and hence protected from continuous roadside management. Once *P. setaceum* populations establish, they may persist for years and hence utilise the resources to the detriment of other native species.

The construction of roads and the improvement of existing ones have been highlighted as important factors in the ongoing spread of invasive alien plant species elsewhere (Greenberg *et al.*, 1997; Forman & Alexander, 1998; Trombulak & Frissell, 2000; Gelbard & Belnap, 2003). Our findings are consistent with the idea that the effect of road improvement on plant cover and richness is due to factors associated with road construction and road maintenance and not to differences in site characteristics (there was no relationship between soil type and *P. setaceum* occurrence).

Environmental factors and conditions affecting the distribution of P. setaceum

A large number of factors have been identified that influence the spread and success of invasive species along roads (Milton & Dean, 1998; Gelbard & Belnap, 2003) and rivers (Johansson *et al.*, 1996) in different biomes. We tested the hypothesis that *P. setaceum* would be more prevalent near human settlements where it originates as an ornamental. Contrary to other findings that housing density and their distance from the roads were found to play a major role in explaining alien plant species presence along roads (Harrison *et al.*, 2002; Gelbard & Harrison, 2003; Pauchard & Alaback, 2004; Kalwij *et al.*, 2008), *P. setaceum* did not show any preference to any of the land use types recorded. This suggests that the grass has the potential to disperse and establish far away from the point sources and could invade natural areas in other parts of South Africa.

Although the occurrence of *P. setaceum* was not influenced by soil type, plants in alluvial soils were larger (basal diameter) than on other soil types. This suggests the influence of extra moisture and nutrients, as well as the possible influence of floods that decrease the strength of competitive interactions on these alluvial plains (Hood & Naiman, 2000; Parendes & Jones, 2000; Richardson *et al.*, 2007). This provides an indication of the magnitude of distribution this grass could have, particularly along tributaries and roads that traverse natural areas (Joubert & Cunningham, 2002; Milton, 2004) and into disturbed or sparse vegetation on fertile soils (Williams *et al.*, 1995; Milton *et al.*, 1998). Our results support the idea that roads act as disturbances that promote invasive species (Harrison *et al.*, 2002; Dong *et al.*, 2008), especially at their interchanges with the rivers where we found more propagules produced.

The presence of *P. setaceum* away from the road was associated with the presence of water bodies, such as river systems and animal drinking points. These points provide extra moisture that plants need for continued growth and persistence, especially away from the roads where disturbances may not be prevalent. Disturbances, such as overgrazing, that occur away from the roadsides also facilitate the presence of *P. setaceum*, especially if it also occurs on the roadside nearby.

There are some important caveats to our results. Major roads in South Africa are heavily managed and the grass is cut regularly along the road verges. This means that some populations might have been missed during sampling. Timing of sampling might have played a role in the presence of the grass, the grass is usually visible when it has flower heads (inflorescences) and during dry periods and some populations might have been missed if dry. Some biomes were under-sampled and hence the results obtained may not be generalised. Despite these caveats, our repeatable method could be used for monitoring the spread of this grass and other alien plants in South Africa and elsewhere, especially along roads and rivers. This method is also convenient and efficient, in that it can be performed during overland journeys to other experimental sites.

Alien perennial grasses pose a number of problems to many ecosystems, as a result of their efficient growth and dispersal mechanisms. We suggest that the presence of *P. setaceum* along roadsides will pose a major problem by being able to produce more propagules that will eventually fly and/or float along rivers and roads and establish further and hence expand the grass invasion range. Problems will also arise when colonies expand out from roadsides into agricultural lands and rangelands. Our findings suggest that road-river interchanges should be considered important targets of both local and regional efforts to prevent and control this grass. Management efforts to prevent or slow down the spread of invasive alien species must recognise that communities with fertile rocky soils, such as the Fynbos Swartland Shale Renosterveld vegetation type, are particularly vulnerable to invasion by *P. setaceum* and possibly other similar alien grasses. These results indicate the importance of road-river interchanges as important habitat for the invasive *P. setaceum*. This is important information for its potential distribution and range expansion. Since small populations of this grass at interchanges can easily spread through the same corridors over the landscape, their early detection is crucial for land managers. Our results suggest that the availability of propagules and the ideal conditions (mesic and disturbed) at these interchanges will facilitate the proliferation of other similar invasive alien grasses. Management of these grasses should focus on spot infestations on these interchanges for the better control of this alien invasive grass.

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